



Drought differentially affects the post-fire dynamics of seeders and resprouters in a Mediterranean shrubland

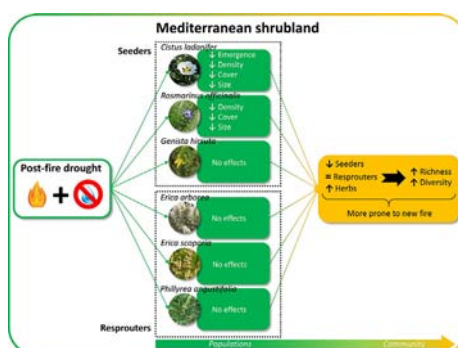
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HIGHLIGHTS

- Post-fire rainfall changes can affect species with different regeneration mode.
- Drought and fire was experimentally imposed to a shrubland.
- Drought negatively affected to seeders but not to resprouters.
- Drought caused a 'herbalization' of the community.
- Future resilience can be compromised by post-fire drought.

GRAPHICAL ABSTRACT



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ABSTRACT

In fire-prone ecosystems, changes in rainfall after fire could differentially affect seeders and resprouters, thus leading to long-lasting impacts on the vegetation. Climate change in the Mediterranean region is projected to reduce precipitation, expand the summer drought and increase fire danger. Understanding the sensitivity to changes in rainfall during the post-fire regeneration stage is critical to anticipate the impacts of climate change on Mediterranean-type areas of the world.

Here, we investigated how species differing in post-fire regeneration strategy (seeders vs resprouters) responded to rainfall changes in a *Cistus-Erica* shrubland of central Spain. Drought treatments were implemented using a system of automatic rainout shelters with an irrigation facility before (one season) and after (four years) burning a set of experimental plots. Treatments applied were: environmental control (natural rainfall), historical control (mimicking the long-term rainfall), moderate drought (−25% rainfall), and severe drought (−45% rainfall). Plant demography and vigour (main woody shrubs), as well as abundance (shrubs and herbs) were monitored during the first four years after fire.

The first post-fire year was the key period for the recovery of seeders (*Cistus ladanifer* and *Rosmarinus officinalis*), and their recruitment, cover and size significantly decreased with drought. However, density four years after fire was larger than unburned and it was significantly correlated with emergence during the first year, indicating that population controls were more on emergence than on establishment. In contrast, resprouters (*Erica arborea*, *Erica scoparia* and *Phillyrea angustifolia*) were hardly affected by drought. Plant community dynamics in the burned control plots progressively converged with the unburned ones, while that in the drought-treated plots lagged behind them, maintaining a higher cover, richness and

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diversity of herbs. This post-fire “herbalization” due to drought might facilitate an untimely fire, before seeders would reach sexual maturity, which could have major implications for the maintenance of the community.

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1. Introduction

Water availability is the most limiting factor in Mediterranean-type ecosystems (Di Castri et al., 1981; Reichstein et al., 2002), where fire is also a key ecological factor (Keeley et al., 2012). The effects of water limitations could be particularly relevant during the early post-fire regeneration stages, since changes at this time in plant composition and/or abundance could have long-lasting consequences for the plant community (Keeley et al., 2005a; Zedler et al., 1983). Moreover, shifts in fuels caused by altered community composition and/or structure could make the system more prone to the occurrence of a new fire and affect the future fire characteristics (Moreno et al., 2013; Strom and Fulé, 2007). Thus, understanding the sensitivity of Mediterranean fire-prone ecosystems to reduced water availability during the early regeneration after fire is particularly important for determining their vulnerability to the combined effects of fire and drought under the ongoing climate change.

In Mediterranean ecosystems, plant regeneration after fire occurs by seed germination (seeders) or by vegetative regrowth (resprouters) (Bond and van Wilgen, 1996). Species within these two regenerative strategies exhibit contrasted morphological and physiological traits regarding their gas exchange, root system and leaf water conservation characteristics (Parra and Moreno, 2017; Pausas et al., 2004; Pausas et al., 2016; Vilagrosa et al., 2014). Therefore, changes in rainfall total or patterns during the year could differentially affect these functional groups. These effects could be particularly important during post-fire regeneration, since early developmental stages of plants are expected to be more vulnerable to changes in climate or other environmental factors than adult stages (Dalglish et al., 2010; Lloret et al., 2004).

Seeder species die during the fire, recovering entirely from seed germination (Keeley et al., 2012). Germination strongly depends on having the appropriate moisture and temperature (Bewley et al., 2013; Chamorro et al., 2017), so seeders are hypothesized to be rather vulnerable during the emergence phase. Once emerged, seedlings are also vulnerable to water stress due to their lower ability to capture resources until their root systems reach a safe depth below the desiccating front into the soil (Moreno and Oechel, 1992; Padilla and Pugnaire, 2007). In fact, seedling emergence and establishment patterns are closely related to post-fire rainfall (Moreno et al., 2011; Quintana et al., 2004), so reduced rainfall and a shorter wet season can lead to lower emergence and lower survival, hence lower plant density. Moreover, since not all species are equally sensitive to such changes (Lloret et al., 2004; Moreno et al., 2011; Quintana et al., 2004), these can lead to alterations in species composition and richness (Liu et al., 2017; Miranda et al., 2009).

In contrast, the post-fire regeneration of resprouter species is not so closely tied to water availability, since resprouts usually experience favourable water status in the months immediately after fire, and independently of rainfall patterns (Castell et al., 1994; Clemente et al., 2005; Fleck et al., 1995). In fact, resprouts can access deep-water sources through the well-developed root system of the surviving individual (Clarke et al., 2013; Cruz et al., 2002), and they can take advantage of the increased water availability during the early stages after fire owing to reduced water interception and transpiration (Silva et al., 2006). Thus, the post-fire functional performance of resprouters has been shown to be highly resistant to drought (Parra and Moreno, 2017), although contrasted results have also been reported when drought severity was extreme (Pratt et al., 2014).

In addition to woody shrubs, herbaceous plants can also be an important component of the plant community (Holzapfel et al., 2006; Seifan et al., 2010), especially during the early stages after fire. Herbs usually have faster growth rates than shrubs and woody seedlings (Sánchez-Gómez et al., 2006), and can outcompete woody shrubs (Davis et al., 1998; Vilá and Sardans, 1999). On the other hand, a high cover of herbs can also ameliorate the microclimate conditions of seedlings during the summer months, for example by providing shade, and thus reducing the stress due to high temperatures and evapotranspirative demands (Brooker et al., 2008; Holmgren et al., 1997). Moreover, herbs can also capture available nutrients that otherwise could be lost with runoff (Rundel and Parsons, 1984; Schlesinger et al., 2000), and thus act as an insurance for later growth of the woody species. That is, herbs can play a negative or positive role on the regenerating community, with higher effects on the seedlings than on the resprouts.

Summer drought is a characteristic feature of the climates bordering the Mediterranean basin, where seasonal and yearly rainfall is also highly variable (Lionello et al., 2006). Moreover, climate change is projected to decrease precipitation in this region, concentrating rainfall towards the winter months, and therefore increasing the summer drought period as well as the frequency and intensity of drought events (Christensen et al., 2013). In parallel, an increase in extreme fire danger is also projected (Bedia et al., 2014), which could increase fire frequency as well as the incidence of large fires (Amatulli et al., 2013). Therefore, the extent of burned areas regenerating under water limitations is projected to increase. Numerous studies have addressed the effect of drought on plants (Beier et al., 2012), as well as on the ecosystem response to fire (Wan et al., 2001). However, there are few field studies that have evaluated the impact of drought on post-fire plant regeneration (e.g. Koerner and Collins, 2014; Pratt et al., 2014), mostly by taking the opportunities provided naturally (e.g. Moreno et al., 2011; Prieto et al., 2009), rather than by addressing this issue experimentally. Yet, understanding the interactions between drought and fire is a key issue for assessing the impacts of climate change on Mediterranean ecosystems.

Here, we present the results of a manipulative field experiment conducted in a Mediterranean shrubland in central Spain where rainfall total and patterns were modified by means of a system of automatic rain-out shelters with an irrigation facility. We simulated various levels of drought by reducing the total amount of annual rainfall and expanding the summer drought period towards spring and autumn. Plots were initially treated from spring until late summer, after which they were burned. Treatments continued for four additional years after fire, during which plant dynamics were monitored. Our aims were: i) to determine the effect of reduced rainfall and increased duration of the summer drought on the post-fire demography of the main woody species in this shrubland; ii) to assess whether plants differing in their regeneration strategy after fire (seeders vs resprouters) responded differently to such changes; iii) to evaluate if the alterations caused in the dynamics of the woody species due to rainfall modifications affected the herbaceous species and the plant community as a whole.

2. Material and methods

2.1. Study area and experimental design

The research was carried out at the Quintos de Mora range station (39°25' N, 4°04' W), located in the Montes de Toledo mountain range

(central Spain). A stand was chosen on a NW-facing 20% slope, at an altitude of 900 m, covered by a dense shrubland dominated by *Cistus ladanifer* L. (Cistaceae, 36% cover), *Erica arborea* L. (Ericaceae, 17% cover), *Phillyrea angustifolia* L. (Oleaceae, 14%), *Erica scoparia* L. (Ericaceae, 12%), *Rosmarinus officinalis* L. (Lamiaceae, 11%), and *Genista hirsuta* Vahl (Fabaceae, 2%). The climate in the area is Mediterranean, with a mean annual temperature and precipitation of 14.9 °C and 622 mm, respectively (Los Cortijos meteorological station, 39°19' N, 4°04' W; AEMET, Spain). Soil is a Dystric Cambisol (IUSS Working Group WRB, 2007), with sandy loam texture and a high proportion of pebbles (Laboratorio Agrario Regional de Albacete; Consejería de Agricultura de Castilla-La Mancha, Spain). The study area (100 × 75 m), which had not been burned or cleared in the last 30 years, was fenced to avoid trampling and herbivory by large mammals. Twenty 6 × 6 m plots were marked and assigned to five treatments, following a randomized complete block design (four blocks with five treatments per block, hence four plots per treatment). Plots were subjected to various rainfall manipulations (see next section) from early spring 2009, and were burned (+) at the end of that summer. Subsequently, rainfall manipulations continued for the next four years. A plot per block was neither manipulated nor burned, serving as unburned control (−) (Appendix A. Fig. S1). Furthermore, to minimize edge effects, plants were sampled using as much as possible the innermost 4 × 4 m area of the plots, or, at most, the 5 m × 5 m central area. Moreover, 1-m wide roofing-type plates were displayed on the surface around each plot to increase the width of the area deprived of rainfall (see Parra et al. (2012) for further details).

2.2. Rainfall manipulation and experimental burning

Based on long-term precipitation records of Los Cortijos meteorological station, close to the study area, and climate change projections of annual precipitation reduction and summer drought lengthening for the Mediterranean (Christensen et al., 2013), four treatments were implemented (Fig. 1a): i) environmental control (EC), that is, natural rainfall without further manipulations (455 mm/year fell on average during the study period, 2009–2013); ii) historical control (HC) (600 mm/year), a simulation of the mean biweekly rainfall pattern recorded in the long-term meteorological dataset of the study area (1948–2006), including 2 months drought per year (July and August); iii) moderate drought (MD), 25% rainfall reduction relative to HC (450 mm/year), with 5 months drought (May to September); iv) severe drought (SD), 45% reduction relative to HC (325 mm/year), with 7 months drought (April to October). To implement these treatments, the rainfall falling onto the plots was controlled in two-week periods by means a rainout shelter system with an irrigation facility. At the beginning of each two-week cycle, natural rainfall was allowed to fall until reaching the level set for each treatment, after which the automatic rainout shelters were programmed to be displayed over the plots in case more rainfall would fall. If the rainfall fallen at the end of each two-week period was insufficient to reach the target, the plots were irrigated with water stored in large containers next to the study plots until reaching the level set for the corresponding two-week period and treatment. It is important to note that, since the treatments remained active >4 years, the magnitude of the droughts imposed was extreme in relation to the historical dataset. Meteorological data were measured with a weather station (Model MTD-3016; GEONICA S.A., Madrid, Spain) placed at the field site. Soil water content was measured with four time-domain reflectometer probes (TDR 100; Campbell Scientific Inc., Logan, UT, USA) installed at each plot down to a depth of 15 cm (Fig. 1b). The high degree of stoniness prevented further penetration of the probes. For further details of the rainfall treatments and manipulation system see Parra et al. (2012) and Parra and Moreno (2017).

The experimental burning was conducted in late summer 2009, 6 months after the beginning of the rainfall manipulations, for which the shelters and irrigation system were dismantled and put in a safe

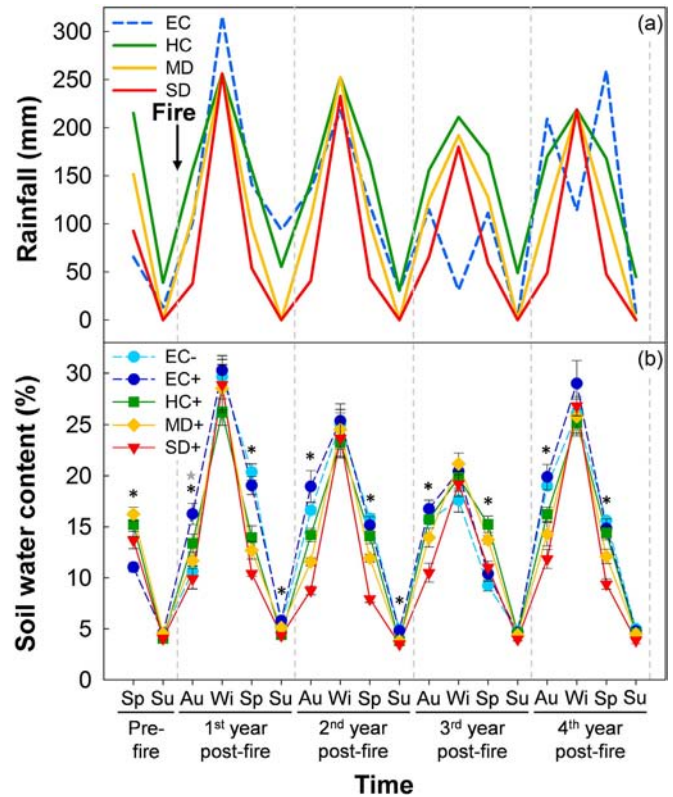


Fig. 1. (a) Rainfall (mm) and (b) volumetric soil water content at 15 cm depth (%) seasonally recorded in the different experimental treatments before and after fire. The acronyms EC, HC, MD, and SD correspond to the different rainfall manipulations applied: environmental control, historical control, moderate drought and severe drought, respectively. The “−” and “+” symbols represent unburned and burned treatments, respectively. Error bars represent standard errors. Stars (*) and asterisks (**) show statistically significant differences among treatments ($P < 0.05$) based on a one-way ANOVA testing, every season, fire effect (EC−/EC+) and post-fire drought effect (EC+/HC+/MD+/SD+), respectively.

place. Later, each plot was burned individually, recording the soil surface temperatures with various thermocouples (HOBO Type K Thermocouple; Onset Computer Corp., Bourne, MA, USA). All plots burned rather homogeneously, with high fire intensity, and no significant differences in various fire intensity measures were recorded among rainfall manipulation treatments (average residence time above 100 °C was 13.5 min, mean maximum temperatures reached was 710 °C). Following the fire, the entire rainfall manipulation system was reinstalled, and manipulations continued for the following four years. For further details of the experimental burning see Parra et al. (2012).

2.3. Vegetation sampling

2.3.1. Seeder species

Nine 50 × 50 cm permanent quadrats, regularly distributed within the innermost 4 × 4 m area of each plot, were set to monitor the woody seeders (*C. ladanifer*, *R. officinalis* and *G. hirsuta*) during the first four years after fire. All seeder plants were killed by fire, and each new seedling was marked at emergence with a coloured pin within the sampling quadrats, and tallied every month until its death or the end of the experiment. Plant emergence (ind. m^{−2}) was obtained as the accumulated number of new individuals emerged throughout every year after the fire, and recruitment (density; ind. m^{−2}) as the number of surviving individuals at the end of each year. Survival (%) was obtained from the recruitment (density)/emergence ratio. Plant cover (%) was visually estimated in the same sampling quadrats every late spring (May–June), at the end of the growing season. Likewise, every season, size (cm) of the various species was measured as the maximum length reached by one

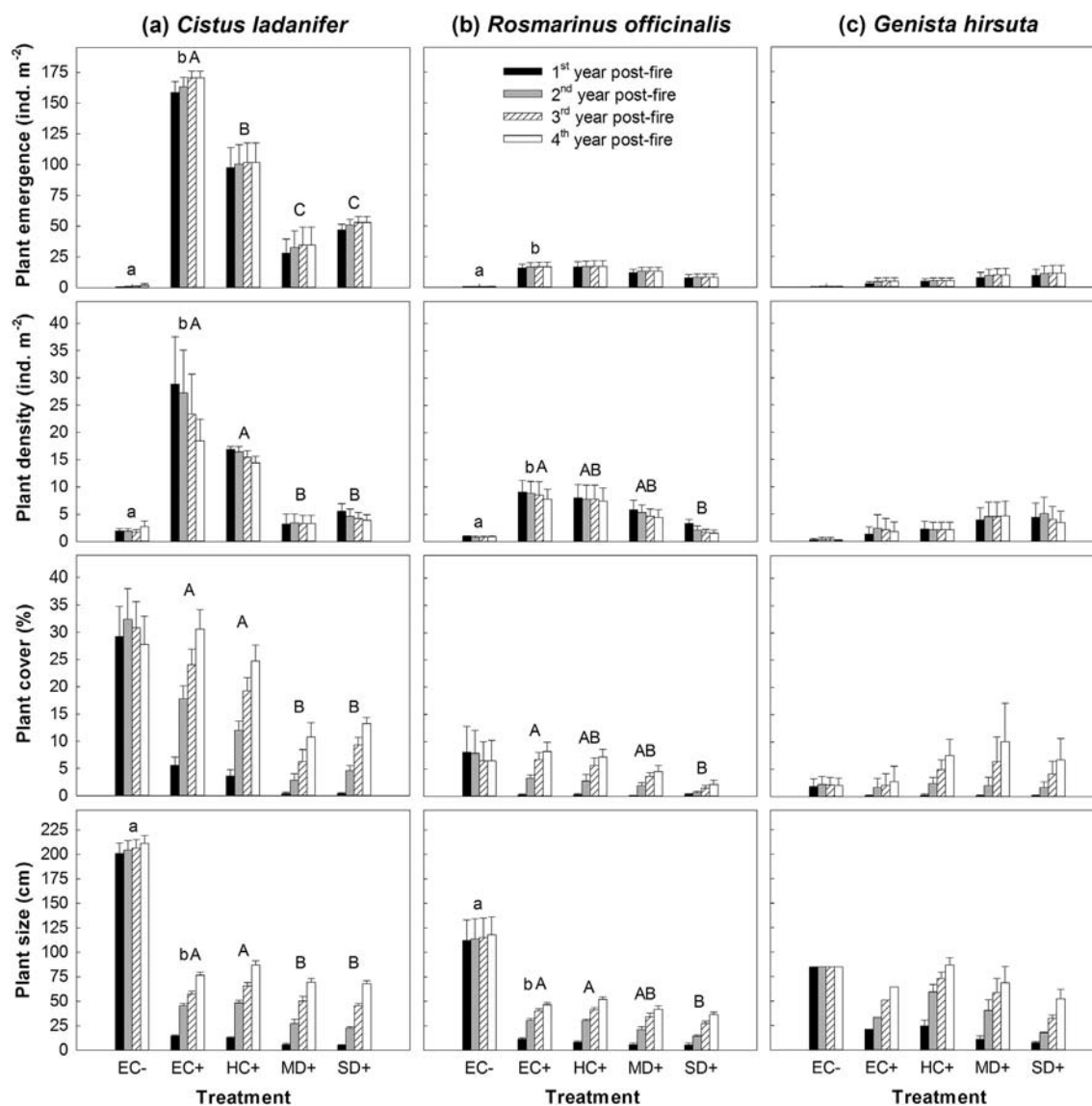


Fig. 2. Plant emergence (ind. m⁻²), density (ind. m⁻²), cover (%) and size (cm) recorded for (a) *C. ladanifer*, (b) *R. officinalis* and (c) *G. hirsuta* in the environmental control unburned (EC–), environmental control burned (EC+), historical control burned (HC+), moderate drought burned (MD+) and severe drought burned (SD+) treatments at the end of the first four years after fire. Error bars represent standard errors. Lowercase letters and uppercase letters represent statistically homogeneous subsets from a repeated measures ANOVA Tukey test assessing fire effect (EC–/EC+) and post-fire drought effect (EC+/HC+/MD+/SD+), respectively. The absence of letters implies that there were no significant differences among treatments ($P > 0.05$).

Table 1
P-values from a repeated measures ANOVA testing fire effect (Fire; EC–/EC+) and post-fire drought effect (Drought; EC+/HC+/MD+/SD+) on plant emergence (ind. m⁻²), density (ind. m⁻²), cover (%) and size (cm) of *C. ladanifer*, *R. officinalis* and *G. hirsuta* throughout the first four years after fire. The acronyms EC, HC, MD, and SD correspond to the different rainfall manipulations applied: environmental control, historical control, moderate drought and severe drought, respectively. The “–” and “+” symbols represent unburned and burned treatments, respectively. P-values ≤ 0.05 are shown in boldface.

	<i>Cistus ladanifer</i>		<i>Rosmarinus officinalis</i>		<i>Genista hirsuta</i>	
	Fire	Drought	Fire	Drought	Fire	Drought
Plant emergence						
Treat. (T)	<0.001	<0.001	0.004	0.293	0.064	0.923
Time (t)	0.042	<0.001	0.060	<0.001	0.100	0.004
T × t	0.079	0.285	0.080	0.467	0.276	0.527
Plant density						
Treat. (T)	<0.001	0.001	<0.001	0.034	0.570	0.862
Time (t)	0.251	0.008	0.226	<0.001	0.258	0.166
T × t	0.052	0.035	0.318	0.008	0.599	0.257
Plant cover						
Treat. (T)	0.114	<0.001	0.538	0.034	0.641	0.746
Time (t)	<0.001	<0.001	0.143	<0.001	0.268	0.002
T × t	<0.001	0.002	0.034	0.013	0.520	0.559
Plant size						
Treat. (T)	<0.001	0.001	0.001	0.019	–	0.099
Time (t)	<0.001	<0.001	<0.001	<0.001	–	<0.001
T × t	<0.001	0.006	<0.001	0.052	–	0.255

tagged individual within each sampling quadrat. Only annual data are used in this study.

3.2.2. Resprouter species

All individuals of the resprouter species (*E. arborea*, *E. scoparia* and *P. angustifolia*) within the innermost 5 × 5 m area of each plot were tagged before fire and monitored during the first four years after fire, since they were top-killed by fire and regrowth later from the lignotubers. Plant survival (%) and density (ind. m⁻²) were measured every month. Plant cover (%) was visually estimated every late spring, using the same sampling quadrats of the seeder species. Likewise, three individuals per species and plot were selected to measure plant size (cm) every season, for which purpose the maximum length reached by any resprout of a given plant was used. Only annual data are used in this study.

3.2.3. Plant community

Every late spring during the first four years after fire, plant cover (%) was visually estimated for each species (woody and herbaceous) present in the sampling quadrats. Additionally, plant cover was also separately estimated for all woody or herbaceous species, each as a distinct group. Based on these estimates, we later calculated species richness, and Shannon diversity and evenness indices for each plot. Species richness per plot was derived from the total number of species appearing in all nine sampling quadrats. Likewise, diversity and evenness indices were derived based on presence/absence and abundance data in all nine sampling quadrats per plot.

2.4. Statistical analysis

One-way repeated measures ANOVA and post-hoc SHD Tukey test were conducted to assess the effects of fire (test EC−/EC+) and post-fire drought (test EC+/HC+/MD+/SD+) on plant emergence, survival, density, cover and size of *C. ladanifer*, *R. officinalis*, *E. arborea*, *E. scoparia* and *P. angustifolia* throughout the four first years after fire ($n = 4$ per treatment). Additionally, one-way ANOVA and subsequently post-hoc SHD Tukey test were conducted to test the effects of fire and post-fire drought on soil water content, woody and herbaceous cover, plant species richness and diversity at each sampling time. Prior to statistical analysis, block effects and pre-fire covariates (plant density, cover and size) were included in the corresponding analysis. However, none of these were significant, and thus were excluded from later models. All analyses were implemented in SPSS v. 19.0 Package for Windows (IBM Corp., Armonk, NY, USA).

The relationship between seedling emergence and recruitment (density) of the seeder species at the end of the four years after fire, and the differences among them were evaluated by using ordinary least square regressions and a test for homogeneity of slopes (ANCOVA). Changes in plant community composition over the years were assessed by a non-parametric multivariate analysis of variance (PERMANOVA; Anderson, 2001), using the individual cover values of each and every species (woody and herbaceous) and the Euclidean distance as dissimilarity measure. To facilitate interpretation of the plant community dynamics, we performed a non-metric multidimensional scaling (NMDS) ordination (Clarke, 1993), again using all individual cover values (woody and herbaceous) and Euclidean distance as dissimilarity index. All of these analyses were carried out with the PAST computer package (Hammer et al., 2001).

3. Results

3.1. Rainfall and soil moisture

Natural rainfall, that is, that falling onto the non-manipulated plots (EC), was highly variable, with a maximum of 652 mm during the first post-fire year, higher than that the long-term average (HC), and a minimum of 366 mm during the third post-fire year, which was even lower

than SD during part of the year when this occurred (Fig. 1a). The manipulations were effective in decreasing total rainfall falling onto the drought plots, and in progressively increasing the duration of the drought period (HC < MD < SD) (Fig. 1a). Soil water content in the upper layers was significantly different among treatments in spring and autumn of the four first post-fire years, the lowest values corresponding to SD+, intermediate in MD+ and highest in HC+, with those of EC+ varying depending on the year. Significant differences in soil moisture between EC− and EC+ were found only during the first autumn (Fig. 1b).

3.2. Woody seeders

Under natural rainfall, fire had a significant effect on the emergence and recruitment (i.e., density) of *C. ladanifer*, showing 85-, and 7-fold significantly higher rates in the burned (EC+) than in the unburned (EC−) plots, respectively, four years after fire. Plant cover reached similar values between both treatments at the end of the experiment, although plants in the burned plots had not even reached half the size of the unburned plants in that period (Fig. 2a; Table 1; Table S1). On the other hand, the drought treatments (MD+ and SD+) significantly reduced emergence and recruitment by over a third with respect to both environmental and historical control treatments (EC+ and HC+), although density in the drought treatments was still higher than in the unburned plots (EC−) four years after fire. Plant cover and size in the drought treatments were also significantly lower (about 12% and 68 cm, respectively) than in the control ones (about 27% and 81 cm, respectively) at the end of the experiment (Fig. 2a; Table 1; Table S1).

R. officinalis showed a similar pattern of response to *C. ladanifer*. We found 27-, and 8-fold significantly higher emergence and recruitment in burned (EC+) than in unburned (EC−) plots, respectively, four years after fire. Likewise, plant cover was similar in the burned plots than in the unburned ones at the end of the experiment, although plants in the burned plots were still half the size of those in the unburned plots (Fig. 2b; Table 1; Table S1). Rainfall manipulations caused a significant and progressive decrease, from the control plots (EC+, HC+) to those with severe drought (SD+), in plant density (from around 7.5 in EC+ and HC+ plots to 1.5 ind. m⁻² in SD+), cover (from 7.5 in EC+ and HC+ to 2.2% in SD+) and size (from 48 in EC+ and HC+ to 36.3 cm in SD+) four years after fire (Fig. 2b; Table 1; Table S1).

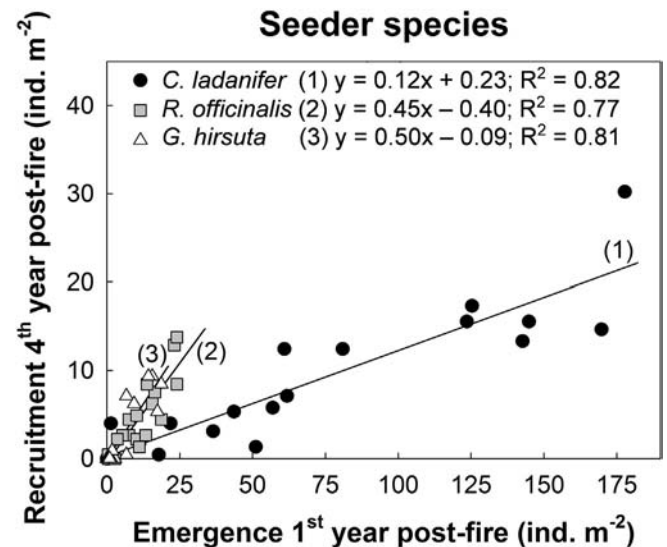


Fig. 3. Linear least squares regression between the emergence recorded during the 1st year after fire and the recruitment (density) finally obtained at the end of the 4th year after fire for *C. ladanifer*, *R. officinalis* and *G. hirsuta*.

As for *G. hirsuta*, we did not find significant differences in any measured variables between burned (EC+) and unburned (EC−) plots (the reduced number of individuals in the study plots prevented a statistical analysis only in the case of plant size). Furthermore, no statistically significant differences were observed among rainfall manipulation treatments (Fig. 2c; Table 1; Table S1).

Overall, *C. ladanifer* showed an emergence and recruitment much higher than *R. officinalis* and *G. hirsuta*, as well as higher cover and size four years after fire (Fig. 2). Most emergence and recruitment occurred during the first year in all three species. In fact, >90% of seedlings emerged during the first year after fire in *C. ladanifer* and *R. officinalis*, and over 75% in *G. hirsuta*. Moreover, there was a significant linear relationship between 1st post-fire year emergence and 4th post-fire year recruitment in the three species (Fig. 3), although they differed in the slope of such regressions. *C. ladanifer* had a lower survival (11%), than *R. officinalis* and *G. hirsuta* (about 40%) (Table S2).

3.3. Woody resprouters

E. arborea and *E. scoparia* showed a similar pattern of response to fire and post-fire drought throughout the study period. Post-fire survival was high in the two *Erica* species (overall average from all burned treatments about 80–90%), and thus they had similar densities to unburned plants during the first year after fire, with little change thereafter (Fig. 4a, b; Table 2; Table S1). In contrast, fire had a negative effect on plant cover of both species, this being particularly significant in *E. arborea*, with cover values of 20.9% in EC− plots compared to no >4.1% in EC+, and a size in the burned plants of hardly half of those unburned by the fourth year after fire (Fig. 4a). Likewise, plant size in *E. scoparia* was significantly lower in burned (EC+) than in unburned (EC−) plots four years after fire (Fig. 4b). Post-fire drought did not significantly affect any of the variables measured (Table 2; Table S1).

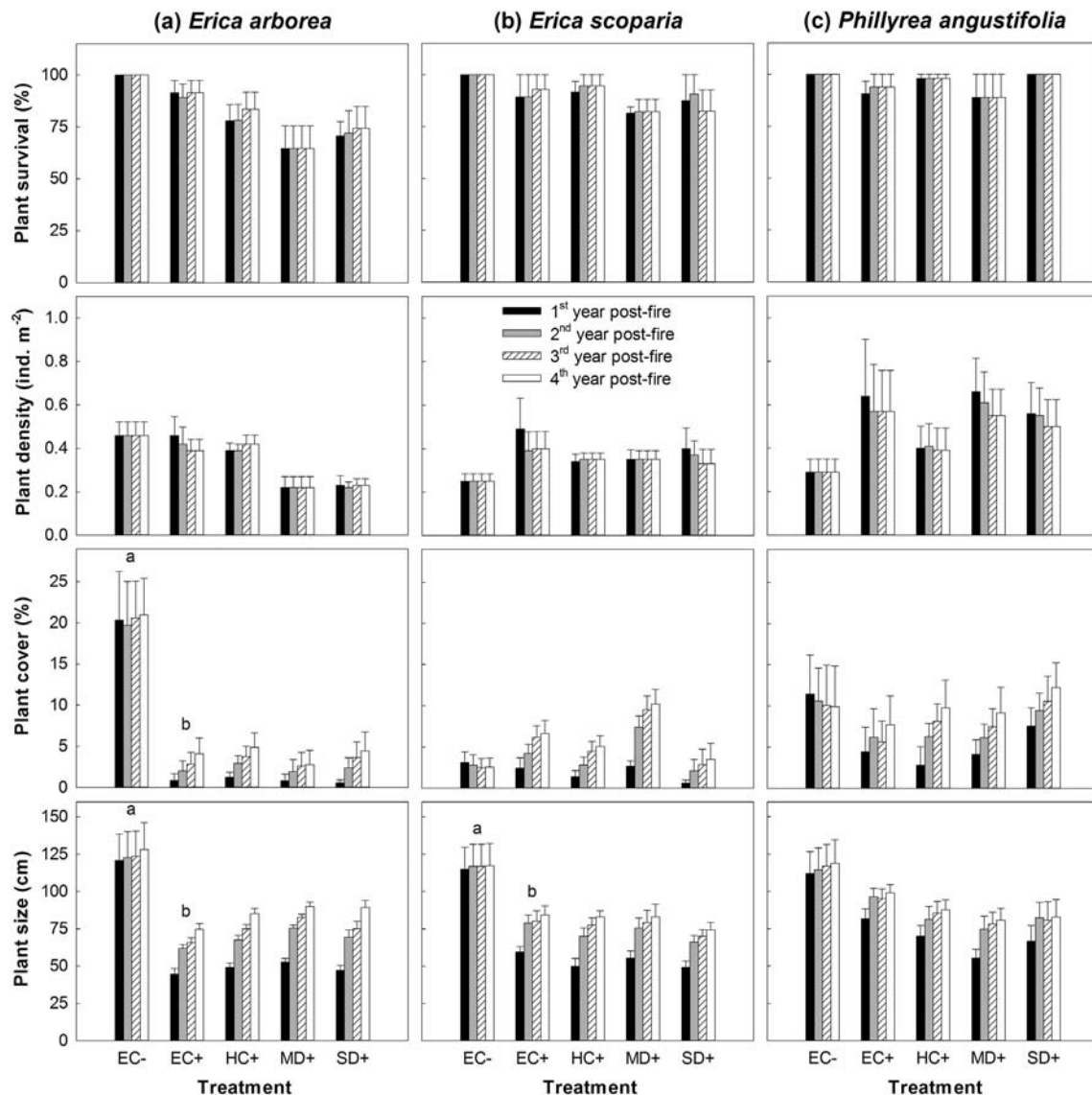


Fig. 4. Plant survival (%), density (ind. m⁻²), cover (%) and size (cm) recorded for (a) *E. arborea*, (b) *E. scoparia* and (c) *P. angustifolia* in the environmental control unburned (EC−), environmental control burned (EC+), historical control burned (HC+), moderate drought burned (MD+) and severe drought burned (SD+) treatments at the end of the first four years after fire. Error bars represent standard errors. Lowercase letters and uppercase letters represent statistically homogeneous subsets from a repeated measures ANOVA Tukey test assessing fire effect (EC−/EC+) and post-fire drought effect (EC+/HC+/MD+/SD+), respectively. The absence of letters implies that there were no significant differences among treatments ($P > 0.05$).

Table 2

P-values from a repeated measures ANOVA testing fire effect (Fire; EC−/EC+) and post-fire drought effect (Drought; EC+/HC+/MD+/SD+) on plant survival (%), density (ind. m^{−2}), cover (%) and size (cm) of *E. arborea*, *E. scoparia* and *P. angustifolia* throughout the first four years after fire. The acronyms EC, HC, MD, and SD correspond to the different rainfall manipulations applied: environmental control, historical control, moderate drought and severe drought, respectively. The “−” and “+” symbols represent unburned and burned treatments, respectively. *P*-values ≤0.05 are shown in boldface.

	<i>Erica arborea</i>		<i>Erica scoparia</i>		<i>Phillyrea angustifolia</i>	
	Fire	Drought	Fire	Drought	Fire	Drought
Plant survival						
Treat. (T)	0.183	0.231	0.356	0.685	0.288	0.616
Time (t)	0.356	0.253	0.356	0.702	0.356	0.337
T × t	0.356	0.813	0.356	0.575	0.356	0.426
Plant density						
Treat. (T)	0.688	0.080	0.141	0.836	0.255	0.819
Time (t)	0.852	0.487	0.283	0.140	0.679	0.061
T × t	0.289	0.096	0.283	0.306	0.679	0.672
Plant cover						
Treat. (T)	0.010	0.811	0.273	0.066	0.381	0.591
Time (t)	0.013	<0.001	0.014	<0.001	0.471	<0.001
T × t	0.086	0.810	0.003	0.047	0.251	0.071
Plant size						
Treat. (T)	0.013	0.067	0.042	0.551	0.209	0.377
Time (t)	<0.001	<0.001	0.001	<0.001	<0.001	<0.001
T × t	<0.001	0.033	0.003	0.411	0.003	0.033

On the other hand, neither fire nor post-fire drought significantly affected any of the measured variables in *P. angustifolia*. Survival was very close to 100% and density was 0.5 ind. m^{−2} (overall average from all burned treatments), slightly higher than that observed in the two species of *Erica*. Moreover, this species had attained similar values of cover (9.7%) and size (87.5 cm) to those unburned by the end of the first year after fire (Fig. 4c; Table 2; Table S1).

3.4. Herbs

A total of 102 species were recorded in all study plots throughout the first four years after fire. The majority of these species were herbs (86%), being annuals (i.e., therophytes) the most frequent (59%). From a functional point of view, we found lower number of grasses (25%) than forbs (75%), although the grasses had higher presence in the community in terms of plant cover (Table S3; Table S4).

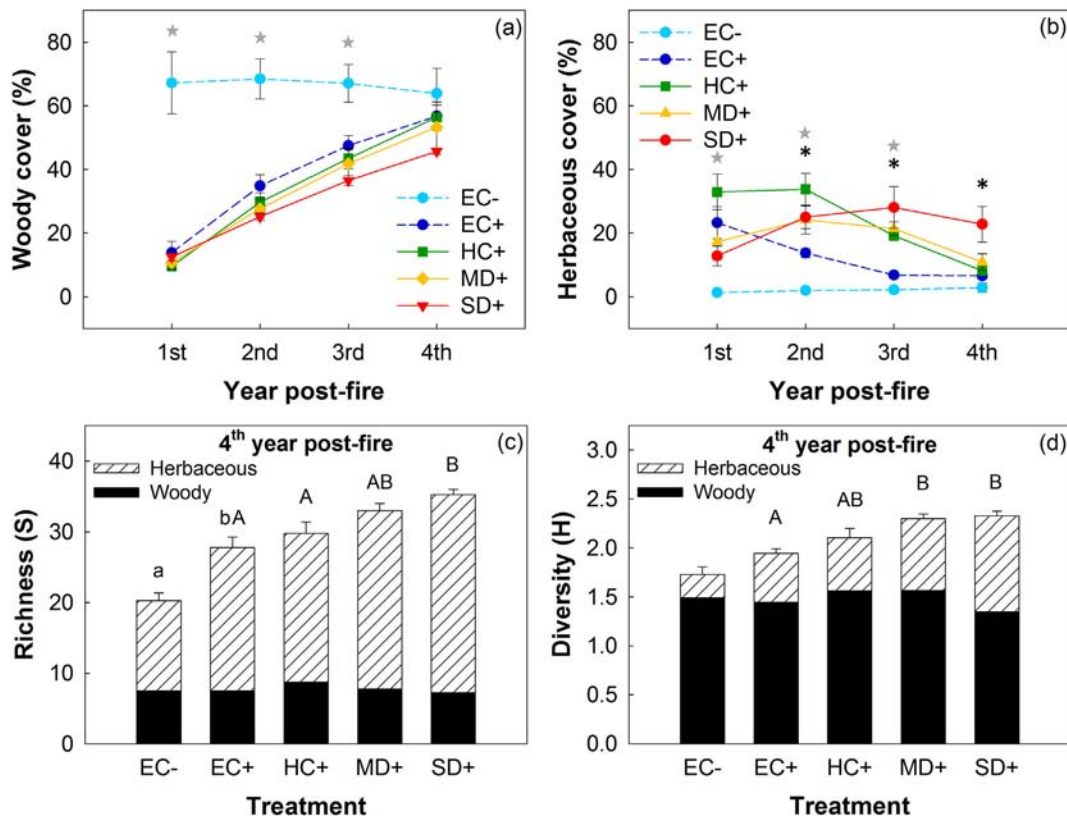


Fig. 5. (a) Woody and (b) herbaceous cover (%) in the environmental control unburned (EC−), environmental control burned (EC+), historical control burned (HC+), moderate drought burned (MD+) and severe drought burned (SD+) treatments throughout first four years after fire. Stars (☆) and asterisks (*) show statistically significant differences among treatments ($P \leq 0.05$) from a one-way ANOVA testing, every year, fire effect (EC−/EC+) and post-fire drought effect (EC+/HC+/MD+/SD+), respectively. (c) Richness and (d) diversity in the different treatments recorded the 4th year after fire. Lowercase letters and uppercase letters represent statistically homogeneous subsets from a one-way ANOVA Tukey test assessing fire effect (EC−/EC+) and post-fire drought effect (EC+/HC+/MD+/SD+), respectively. The absence of letters implies that there were no significant differences among treatments ($P > 0.05$).

The herbaceous cover was significantly higher in the burned plots (EC+) than in unburned ones (EC−) during the first year after fire. Subsequently, the differences between EC− and EC+ treatments progressively diminished as cover of the woody species developed in the burned plots, disappearing completely by the fourth year after fire (Fig. 5a, b). As for the effects of post-fire drought, the herbaceous cover recorded a maximum in HC+ and MD+ treatments (about 30–40%) during the second year after fire, thereafter progressively decreased. However, SD+ treatment recorded a maximum during the third year after fire, and a cover significantly different from HC+ by the fourth year after fire (Fig. 5b). The differences between HC+ and SD+ treatments were mainly due to the high cover of graminoid therophytes recorded in SD+ plots during the fourth year after fire (Table S4).

3.5. Plant community

NMDS ordination showed that unburned plots were well separated from burned plots (all of which were statistically similar among themselves) during the first year after fire. As the years passed, the dynamics of control (EC+ and HC+) and drought (MD+ and SD+) plots were significantly different, as attested by the PERMANOVA results (Fig. 6; Table S5), except for the fact that all plots within a treatment were becoming more divergent among themselves. The control treatments were progressively converging towards the unburned plots as the woody cover was recovering every year, with no significant differences between EC− and EC+ treatments by the 4th year after fire (Fig. 5; Fig. 6; Table S5). However, the drought treatments remained well separated from the control ones, due to a lower recovery of woody cover and higher presence of herbs (graminoid therophytes) (Fig. 5; Fig. 6; Table S5). In fact, higher richness and diversity were recorded in SD+ treatment compared to control ones by the fourth year after fire (Fig. 5c, d).

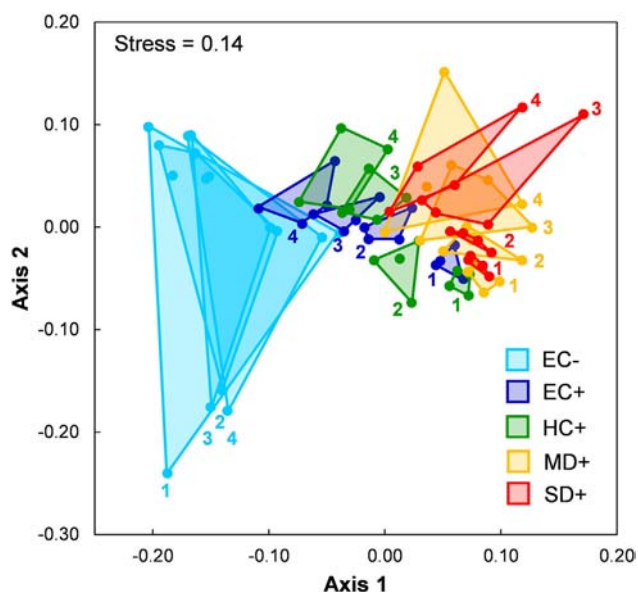


Fig. 6. Two-dimensional NMDS ordination of study plots based on single cover of all species (woody and herbaceous) present in the different treatments throughout the first four years after fire. The acronyms EC, HC, MD, and SD correspond to the different rainfall manipulations applied: environmental control, historical control, moderate drought and severe drought, respectively. The '−' and '+' symbols represent unburned and burned treatments, respectively. Each point represents one of the study plots in the 1st, 2nd, 3rd and 4th year post-fire (indicated by corresponding number). Euclidean Distance was used as dissimilarity index.

4. Discussion

4.1. Seeder species dynamics

Seeders usually increase their density by several orders of magnitude during the first wet season after fire. Seedlings, however, suffer high mortality following emergence, and their density greatly decreases over time (Calvo et al., 2002; Keeley et al., 2006). Nevertheless, at the end of the first post-fire season, it exceeds that before fire (Clemente et al., 1996; Santana et al., 2012), thus allowing full recovery of the population after the fire (Moreno et al., 2011). Likewise, drought significantly affects these early post-fire demographic patterns by reducing emergence and recruitment (Lloret et al., 2009; Prieto et al., 2009). These patterns were observed in this experiment, with a reduced emergence and recruitment in *C. ladanifer* and *R. officinalis* due to drought. Notwithstanding, plant density levels were still higher in burned than in unburned treatments by the fourth year after fire, which led to similar cover in burned and unburned plots in spite of the plant size was negatively affected by drought. That is, the population recovery of the seeder species appeared to be ensured four years after fire even under the most severe drought treatment implemented, at least from a demographic point of view.

Drought reduced emergence and recruitment but did not cause a significant decrease in survival (Table S6). This shows that post-fire environments, once a seedling emerges, are favourable for establishment, regardless of the drought severity. Parra and Moreno (2017) showed that, during the first years after fire, seedling water potential remained high, much more than that of adults, including under drought. Higher water availability due to increased throughfall and reduced transpiration by a limited leaf area during the first stages of regeneration (Silva et al., 2006) would counter the negative effects of drought. This effect would remain effective until the transpiring surface would be recovered, which, paradoxically, would be delayed due to drought owing to limited plant emergence and growth. In fact, it has been shown that drought significantly reduces the leaf transpiring area in the Mediterranean forest (Limousin et al., 2009). Therefore, the window of opportunity for seedlings to establish due to the ameliorated water conditions caused by fire would be extended by drought. Once the community recovers its transpiring surface, the sensitivity to drought would also recover, as shown by the high sensitivity to drought in the adult, pre-fire community (Parra et al., 2012; Ramírez et al., 2012).

We also found that the first year after fire was the key temporal window for post-fire regeneration of the seeder species, since most emergence and recruitment occurred in that period, as reported earlier in this system (Moreno et al., 2011; Quintana et al., 2004) and in other Mediterranean areas (Keeley et al., 2005b). This pattern was common in all burned plots, which means that seeds in the drought-treated plots that did not germinate during the first year did not germinate at all. In accordance with this, we found a positive correlation between emergence in the first year and recruitment at the end of the fourth year after fire in all seeder species, despite the implemented drought treatments. This supports earlier findings by Moreno et al. (2011) and reinforces the idea that emerging early gives the plants a competitive advantage (De Luis et al., 2008), in such a way that what happens during the first year post-fire is critical for the long-term fate of the populations of these species. Therefore, since population controls rested largely on emergence, not so much on survival and subsequent recruitment, further understanding is needed about how emergence is controlled under variable rainfall patterns. In fact, it has been recently shown that the sensitivity of some Mediterranean seeders to germinate in response to variations in moisture vary among species (Chamorro et al., 2017).

Nevertheless, while all seeders generally responded as described above, there were also some differences among them. Total plant emergence and recruitment were much higher for *C. ladanifer* than for *R. officinalis* and *G. hirsuta*. The larger production of seedlings in *C. ladanifer*

was followed by a lower survival, and only 11% were finally established at the end of the post-fire year after fire. In contrast, *R. officinalis* and *G. hirsuta* showed a pattern in which seedling emergence was much lower, but with a higher survival rate (40%). These differences in survival among species support earlier findings by Quintana et al. (2004), and could be explained by the fact that the seeds of *C. ladanifer* are smaller than those of the other two species. In fact, it has been documented that large-seeded plants are able to better withstand stressful environmental conditions during the early phases of development than small-seeded ones (Armstrong and Westoby, 1993; Jurado and Westoby, 1992).

In brief, our results indicate that the seeder species are rather resilient to fire, even though their post-fire regeneration is negatively affected by drought. Our findings may be applicable to a majority of situations under the current or future climate, given the severity of the treatments implemented (the MD and SD treatments represent percentile 8 and 2 of the historic meteorological series in annual terms, but drought events never occurred during 5 consecutive years in the study area). However, Pratt et al. (2014) observed that pre-fire density of some species in southern California chaparral was not replenished after a fire followed by a drought with a precipitation levels several times below those implemented here. How frequent will appear such levels of drought will vary depending on the magnitude of climate change and on the precipitation variability in a given area (Cowling et al., 2005), as well as the combined effect of temperature and rainfall (Diffenbaugh et al., 2015). That means that a similar decrease in rainfall due to climate change may represent different probabilities of drought hazard in different areas of the world.

4.2. Resprouter species dynamics

Mediterranean resprouter shrubs have been reported to be highly resilient to fire (Calvo et al., 2002; Céspedes et al., 2014a; Konstantinidis et al., 2005). Accordingly, the resprouter species in this experiment were also little affected by fire and, unlike the seeders, the first year after fire was not critical for the recovery of these species. *P. angustifolia* was the most resilient species, since we could not find significant differences between burned and unburned plots for any of the measured variables at any time. This species had almost 100% survival, and rapidly recovered levels of density, cover and size similar to those of the unburned plants, as reported in other studies (Capogna et al., 2009; Vitale et al., 2007). Similarly, survival and density of the two *Erica* species were not significantly affected by fire. A caveat in our findings is that the individuals present in the plots were of large size, and mortality is commonly size dependent in *Erica* species (Canadell et al., 1991). However, the resprouts of these species did not reach a similar size than unburned adult plants during the first four years after the fire, as reported by Céspedes et al. (2014a) and Lloret and López-Soria (1993) in other *Erica* species. This response could be explained by the low growth rates recorded in the *Erica* species both before and after the fire in the study area (Parra and Moreno, 2017; Parra et al., 2012; Ramírez et al., 2012).

It has also been suggested that resprouter species have a high resistance to drought and that the impact of increased drought stress in ecosystems dominated by these species may be small (Zeppel et al., 2014). In our case, none of the analysed variables in the resprouter species were affected by the post-fire drought treatments implemented. As with the seeders, this response is attributed to the ameliorated water conditions after fire (Silva et al., 2006), which allow resprouts to show favourable water status just after the fire (Clemente et al., 2005). In fact, Parra and Moreno (2017) showed that water potential in these species was very high and hardly affected by drought during the first years after fire. Moreover, resprouters can mobilise carbohydrates to sustain plant growth during the early phases of regeneration (Clarke et al., 2013; Cruz et al., 2002), which could help the plant to keep growing even under drought conditions.

While the three resprouter species responded similarly, there were also some differences among them, particularly between both *Erica* species and *P. angustifolia*. In that sense, *E. arborea*, which was found more sensitive to drought than *P. angustifolia* both before (Parra et al., 2012; Ramírez et al., 2012) and after the fire (Parra and Moreno, 2017), showed reduced (albeit not statistically significant) survival and density rates in the drought treatments compared to control ones. Moreover, both *Erica* species had a low post-fire recovery in terms of cover and size, showing that although resprouters are generally quite resistant to drought, their sensitivity may vary depending on the species and the intensity of the drought, which support the findings of Pratt et al. (2014) for southern California chaparral.

4.3. Plant community

Climate-induced changes in species composition and abundance may alter complex networks of species interactions and cause significant shifts within communities (Chapin III et al., 2001). Changes in fire characteristics and weather and climate patterns can differentially affect seedlings and resprouts, thus promoting long-term changes in the community (Moreno and Oechel, 1992; Pausas et al., 2004). Our results showed contrasting responses to drought after fire between seeder and resprouter species, which indirectly affected the dynamics of the herbaceous layer and led to visible differences among treatments at the community level during the first four years after fire. During the first year, the plant community in all burned plots, irrespective of the drought treatments, was very similar among them and clearly different from the unburned plots, which was mainly due to the low cover of woody species. In the following three years, the dynamics of control (EC+ and HC+) and drought (MD+ and SD+) plots was clearly different. Control treatments progressively converged with the unburned plots, because woody cover recovered while herbaceous cover decreased, since both variables are negatively correlated (Casado et al., 2004; Céspedes et al., 2014b). However, drought treated plots slowly diverged from the control ones due to the fact that the cover of seeders was not recovering over time as in the control plots. This low density and cover of seeders, especially *C. ladanifer*, led to a decrease in woody cover and therefore an increase of herbaceous species cover, particularly therophytes, in the most severe drought plots relative to control ones during the 3rd and 4th year after fire. That is, the most severe drought treatment led to a “herbalization” of the plant community, thus presenting a higher richness and diversity in than in control treatments during the 4th year after fire. This increase in richness and diversity due to drought differs from the varied response observed in different shrublands and heathlands in Europe (Peñuelas et al., 2007), and it is the opposite of those reported by Liu et al. (2017), Lloret et al. (2004) and Prieto et al. (2009) in other Mediterranean shrubland. This heterogeneity in the response indicates that regeneration of the plant community after fire depends largely on the vegetation type (Arnan et al., 2007) and the successional stage, and that drought can play different roles depending on whether a rich herbaceous layer is present or not following fire.

Overall, our study shows that drought during the first post-fire years can importantly and differentially affect the regeneration of shrubby species differing in regeneration mode in Mediterranean shrublands. Effects were greater in species having a seeder strategy than in those with a resprouter one. Despite water limitations, seeders, once emerged, were able to establish. Thus, population control is dependent on emergence, no so much on establishment, and it is not altered by drought. Moreover, changes at the population level in some species will further affect the community by altering the dynamics of herbs due to higher availability of space for them as a result of drought. This could further affect the functioning of the ecosystem. In fact, the “herbalization” of the community under severe drought conditions detected during the first years after fire could make the system more prone to the occurrence of a new fire, with the consequent long-term implications. This would

be particularly important if the period between fires were not sufficient for seeders to reach sexual maturity (around three years in our study) and thus to replenish the seed banks of these species (Zedler et al., 1983). Climate change, with its alterations of rainfall total and patterns, and an increase of the drought and fire danger, has the potential to alter shrublands (Enright et al., 2015), extensive in the Mediterranean basin and in other Mediterranean-type climate areas of the world (Di Castri et al., 1981), by favouring resprouters over seeders. In addition, increases in fire frequency driven by higher abundance of herbs in post-fire drought-affected areas could likely add further risk to the integrity of these ecosystems.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.01.174>.

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